Vol. XL. *April, 1921.* *No. 4.*

BIOLOGICAL BULLETIN

AUTHOR'S ABSTRACT OF THIS PAPER ISSUED BY
THE BIBLIOGRAPHIC SERVICE, MARCH 14, 1921.

THE ECOLOGY AND LIFE-HISTORY OF AMPHIGONOPTERUS AURORA AND OF OTHER VIVIPAROUS PERCHES OF CALIFORNIA.

CARL L. HUBBS,

MUSEUM OF ZOÖLOGY, UNIVERSITY OF MICHIGAN.

TABLE OF CONTENTS.

INTRODUCTION.

As the life-history of these fishes is intimately correlated with their viviparity, it may be of interest and pertinence to consider first some of the main features of viviparity in fishes. Most fishes are characterized by the prolific production of ova that are fertilized in an almost fortuitous manner. Within the group, however, some form of protection of the eggs has become repeatedly evolved, in correlation with a decrease in the number of ova and with a less random fertilization. This protection is variously accomplished by one or both parents,—by the burying of the eggs in relatively safe situations; the construction of nests of gravel, plants or bubbles; the driving of predatory

enemies away from the eggs or young; the gestation of the young within the mouth or blood pouch; the enclosure of the eggs in a tough capsule, or finally by the actual development of the young within the oviduct or ovary of the mother.

The degree to which this viviparity has become perfected varies widely in the different groups of viviparous fishes. Some teleosts, such as the scorpænoid fishes, give birth to thousands of minute embryos, still nourished by a relatively large yolk-sac; while others bear only a few young, but fully developed and capable of self-support, almost immediately after birth, in the normal manner of adult fishes. In some of these, as the Pœciliidæ, the embryos are nourished by the yolk in the egg, and a meroblastic type of cleavage persists. In the Embiotocidæ or viviparous perches on the other hand, the yolk is greatly reduced in bulk, the cleavage approaches the holoblastic type (according to Eigenmann, 1894, etc.), and the embryos are profoundly modified structurally.

The viviparous perches (see Figs. 1 and 2) comprise a compact group, the family Embiotocidæ (and the suborder Holconoti) of the Acanthopterygii or spiny-rayed fishes. The group is relatively old, apparently, for the many structural features correlated with viviparity are common to all of the species, and hence became fixed before the extensive generic differentiation characteristic of the family arose. Almost all of the species are generically distinct from the others, another situation suggesting the age of the group (cf. Eigenmann and Ulrey, 1894; Jordan and Evermann, 1898, and Hubbs, 1918). The immediate relationships of the Embiotocidæ not being apparent, nothing definite can be said concerning the origin of their viviparity.

The viviparity of the embiotocids was first definitely made known by Dr. A. C. Jackson in 1853, in a letter to the elder Agassiz. These fishes then almost immediately attracted the attention and study of a number of zoologists, among whom may be mentioned both Louis and Alexander Agassiz, Gibbons, and Girard. Later Ryder, and particularly Eigenmann, studied their embryology, and Jordan and Gilbert, Eigenmann and Ulrey and others also studied the group (see bibliography). I have re-

cently reviewed the family from a taxonomic standpoint (Hubbs, 1918), and have studied the life-history of several species, that of *Amphigonopterus aurora* (Fig. 2) in greatest detail. Although the following account is largely based on this species, comparisons with others are made in several connections.

Ecology.

Nothing whatever has been written concerning the life-history of *Amphigonopterus aurora,* the only species of the genus, and all that has been printed concerning its environmental relations is the statement that it is an inhabitant of the tide-pools of Monterey Bay, California, and that it feeds on algæ. Its habit of feeding

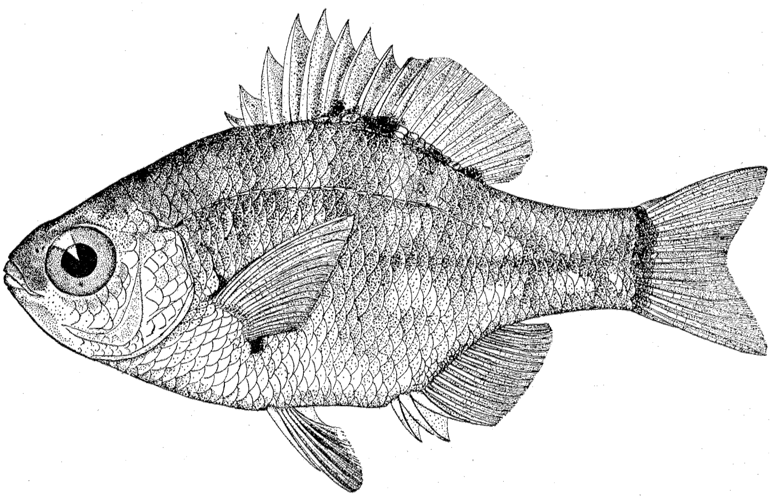

Fig. 1. Adult female of *Micrometrus minimus.*

on algæ, except when very young, when I found it feeding on copepods, is correlated with its tricuspid teeth and comparatively elongate intestine. Similarly I found that the related *Micrometrus minimus* (Fig. 1), though chiefly herbivorous, feeds on small crustaceans when young (Pt. Loma; December 31), and occasionally is caught on clam bait when adult. These two species alone comprise a distinct subfamily, the Micrometrinæ, which I have recently distinguished (Hubbs, 1918).

Amphigonopterus aurora inhabits the tidal pools and channels

along the rock-bound portions of the central California coast, its habitat differing widely from that usual to the species of the family, most of which live in the surf along sandy beaches, or in sheltered bays. In the preference of this species for this extreme type of habitat it is perhaps most nearly approached by *Micrometrus minimus*. The associational distribution of even these two species is, however, imperfectly complementary. Both range from the region of San Francisco southward in the cold coastal waters of central California to the reefs about Point Conception, where the habitat of *A. aurora* is abruptly terminated, whereas that of *M. minimus* is continued southward in the relatively warm waters along the coasts of southern and of Lower California. *Micrometrus minimus* is in fact most abundant in the warmer southern portion of its range, although fairly common northward, where the ranges of the two species coincide. Here, however, *M. minimus* occupies to a large extent a biotic association different from that of its congener, but adjacent to it: it lives and breeds in or not far below the lowermost tide-levels, mostly in the low, deep, plant-filled pools of the reefs (but also in enclosed bays and *esteros*). *Amphigonopterus aurora*, in contrast, is restricted to the reefs, and while breeding at times even in the same pools with its relative, more commonly lives and breeds in the pools and channels of medium tidal height, particularly those that are largely open, free of eel-grass and algæ, and floored with sand. The breeding season of *Amphigonopterus*, moreover, appears to begin earlier than that of *Micrometrus* in central California (see following section). Both of these fishes were found associated in the lower outer rock-pools of the California reefs with the following other species of the family: *Embiotoca jacksoni, E. lateralis, Hypsurus caryi* and *Cymatogaster aggregatus*.

In these open pools the fishes of this species swim about freely in schools[1] at low-tide, occupying the mid-water stratum chiefly,

[1] That these schools of *A. aurora* remain intact for considerable periods of time appears probable from two sets of observations. A number of pools on the reefs just south of Piedras Blancas, and just south of Pt. Sal, by careful observation over a period of several days (during a single series of low-tides in each case), were found to contain many more individuals than any of the adjoining pools, and to contain schools of apparently the same individuals,

occasionally leaping clear of the water (a habit observed only at Pt. Purisima, California, on August 13). During high-tide, however, they must seek the protection of crevices in the sides of the pools, for otherwise they would be dashed about on the rocks by the pounding, churning surf as it breaks on the reefs. In correlation with its preference for pools clearer of vegetation, and with its habits of swimming about rather more freely, *Amphigonopterus aurora* is more extensively silvery than *Micrometrus minimus,* and lacks the dark color pattern characteristic of that species[2] (see Fig. 1). In this connection we should recall that practically all free-swimming or pelagic fishes are silvery and lack the dark markings usually developed in fishes which live among rocks or plants.

Like most reef-fishes examined, *Amphigonopterus aurora* is not heavily parasitized, a fact apparently correlated with the strength of the wave and tidal currents on the reefs. Occasionally, however, a slender lernæan copepod was found attached to the inner surface of the base of the pectoral fin, or to the anal fin near its base.

Breeding Season.

The breeding season of *Amphigonopterus aurora* is the summer, approximately synchronous with that of *Cymatogaster aggregatus,* which breeds in bays and estuaries. It begins shortly before the first of June, as is evident from the observations made on the reefs of Piedras Blancas, California, during the first week of that month. Most of the many females taken on that occasion contained young, relatively few of the largest being spent. Furthermore, all of the hundreds of young in the higher pools were approximately of the size at which they are born. The breeding

judging from the approximate number of the fishes of each size. In a number of pools fished during the summer and fall, the young of the year of each sex were so uniform in size that it seemed probable that they had remained in that pool together since their birth at some time during the breeding season.

2 The most conspicuous color feature of *Amphigonopterus aurora* (the one on which its specific name was based) is the longitudinal band of golden or orange color, which is rarely obsolete (a row of blotches of similar color and position often is present in *M. minimus,* representing this longitudinal band of *A. aurora*). In young specimens the vertical fins are dusky with a reddish tinge, the spinous dorsal, and in the male the anterior portion of the anal fin, being darkest; the pectoral, nearly colorless.

season was found to be still at its height about the middle of July, but to have ended long before October 26.

The breeding season of *Micrometrus minimus* in central California apparently commences somewhat later than that of *Amphigonopterus aurora*. Of females taken in the same pool near Piedras Blancas on June 2, those of *Micrometrus* contained embryos from 4.6 to 18.7 mm. long, none ready for birth, whereas those of *Amphigonopterus* contained embryos 12 to 34 mm. long, the largest obviously ready for birth, being similar to numerous young found at the same locality. A single female of *Micrometrus* collected at Point Purisima, California, on August 14, was spent, but all of those taken during June still contained young. Young showing considerable growth since birth were taken in reef-pools of southern California early in July, suggesting that the breeding season occurs earlier in the warmer waters to the southward.

Sex-ratio in Adults, Young and Embryos.

In the breeding pools poisoned near Piedras Blancas, the females were found to be more numerous than the males, in the proportion of nearly two to one: of those taken (by poison) and sexed, 139 proved to be males; 264, females.[1] An unrecorded observation by Dr. C. H. Gilbert on *Cymatogaster aggregatus* may have some bearing on this point: he has observed a single male "herding about" several females. On the contrary I observed several small fishes of the same species, presumably males, accompanying a mating pair (Hubbs, 1917). However this may be, the numbers of the sexes of the young fishes were found to be approximately equal in two pools at different localities fished in the autumn, after the close of the breeding season: in these two pools, 83 young males and 82 young females were obtained. The 35 adult specimens of *Micrometrus minimus* obtained in a single pool near Piedras Blancas comprised 19 males and 16 females.

A more accurate sex-ratio can be obtained by determining the sex of a series of embryos, by means of the secondary differences in the anal fin, which become clearly evident very early in the

[1] This difference in the sex-ratio may be determined by the greater longevity of the females.

development of *Amphigonopterus* and *Micrometrus* (see next section and Fig. 2). Of 630 embryos of *Amphigonopterus aurora* (from mothers one to four years old), 337 were found to be males, 293 females (sex-ratio: 100 males to 87 females); the ratio does not vary with the age of the parent fishes, being 100 to 86.5 in the embryos from the yearling females only. Of 150 embryos of *Micrometrus minimus* examined, 76 were males, 74 females; the proportion of males to females in each of the seven cases included was, 7 to 9, 9 to 14, 10 to 12, 10 to 13, 11 to 8, 13 to 12, 16 to 6. No tendency toward uniformity in sex even of embryos lying within the same ovarian sheets was evident; hence

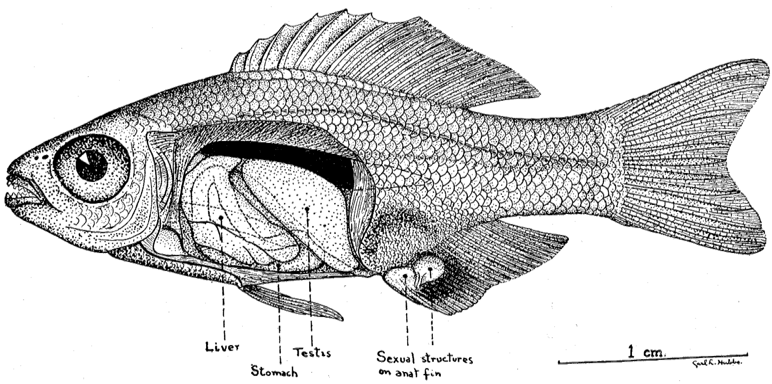

FIG. 2. Newly-born young male of *Amphigonopterus aurora,* from near Piedras Blancas, Cal. Dissected to show mature development of testes.

polyembryony does not occur. Eigenmann recorded similar data for *Cymatogaster aggregatus,* having distinguished the sexes cytologically.

EARLY DIFFERENTIATION OF THE SEXES, AND THE NATAL MATURITY OF THE MALES.

Secondary sexual differentiation is early manifest in the development of *Amphigonopterus aurora* and *Micrometrus minimus.* The differential number of anal rays characteristic of the sexes of each of these two species (Hubbs, 1918) is clearly apparent in embryos only 12 mm. long (the anal rays are first formed when a total length of about 10 mm. has been attained). Eigenmann was unable to distinguish the sexes in *Cymatogaster*

cytologically at earlier stages than this, although he traced the development of the sex-cells from much smaller embryos.

At the 15 mm. stage the sexual differences in the form of the anal fin are also apparent in *Amphigonopterus* and *Micrometrus,* although the gonad remains merely a fine strand of tissue; but at the 20 mm. stage the testes have begun to enlarge, and a slight thickening of the radial membranes marks the position of the

FIG. 3. Section of testis of a newly-born *Amphigonopterus*, showing several stages in spermatogenesis.

elaborate gland developed later on the anal fin of the male. The development of these primary and secondary sexual structures thence rapidly proceeds in *Amphigonopterus aurora* until birth, at which time the gland on the anal fin is fully elaborated (see Fig. 2), and all stages in spermatogenesis from the primordial germ cells to transforming spermatids at least are evident in the testis, the spermatogonia predominating. Just after birth, the

transforming spermatids and spermatozoa appear most abundant (Fig. 3): the testes, as well as the gland on the anal fin, are as well developed in these newly born males, as in the one-, two- and four-year-old males obtained during the breeding season. Both the primary and secondary sexual structures become greatly reduced in size during the autumn, winter and spring of the first, as of the succeeding years. In fact two young males only a few millimeters longer than the birth stage, collected in June, were already "spent." The writer has further determined that the testis becomes similarly enlarged in *Micrometrus minimus* and in *Cymatogaster aggregatus* just before birth. No evidence was obtained, however, to indicate that the males of *Embiotoca lateralis* are mature at birth; even the two one-year-old males of this species (111 and 116 mm. long to caudal) obtained near Pt. Sal, in California, on June 17, with breeding females, were immature. It is quite possible that the natal maturity of the males is confined to the smaller species of the Embiotocidæ.

This natal maturity of the males is particularly significant in view of the fact that the females bear young first at the age of one year. This phenomenon, while unique in the whole class of fishes, so far as the writer is aware, finds a physiological parallel in protandric hermaphroditism, in the frequent early maturing of the male (the "grilse") in the Salmonidæ, and in the earlier seasonal activities of the males of many animals.

Copulation, and the Storage of Spermatozoa.

Dr. Eigenmann (1894, p. 420) summarized one phase of his studies of another viviparous perch with this statement: "*Copulation takes place in Cymatogaster* during June or early July, although the eggs are not fertilized till the following December." He based this conclusion firstly on observations on the seasonal activities of the two sexes, and on the seasonal development of the testes in the male, and secondly, on the discovery of the presence of spermatozoa in the oviduct and in the ovarian folds of the female, during the latter part of the summer, and the autumn. The writer has been able to extend this evidence by the first observation of the copulation of this, in fact of any, embiotocid. The female of the pair in question upon capture was

found to contain only one young, partially protruding from the oviduct, and of the same size as numerous others recently born, found swimming about in the same body of water (Hubbs, 1917).

In *Amphigonopterus aurora* also it is probable that, copulation having taken place during the breeding season in the summer, the spermatozoa are retained in the females until winter (or possibly late autumn or early spring), when fertilization occurs and whence intramaternal development proceeds for several months; and that, therefore, *one year elapses between the time of copulation and the birth of the young.* Six lines of evidence lead to, or are at least not inconsistent with, these conclusions.

1. This condition apparently holds in *Cymatogaster aggregatus*, a distantly related species in which the breeding season is approximately synchronous with that of the present species, the structures correlated with viviparity similar, and in which the adults, and the young at birth, are of similar size to those of *Amphigonopterus aurora.*

2. Females taken in the autumn contained no young, and males secured on October 26, November 25 and April 1 had small and obviously non-functional testes, whereas all of the males taken with the breeding females in the summer had mature testes. This is true also of *Micrometrus minimus,* and perhaps of all embiotocids.

3. The smallest embryos, only 12 mm. long to the caudal fin, taken from any of the females secured in June, would presumably have attained their full embryonic size (about 30 to 35 mm.) late in the summer, toward the end of the breeding season. This fact suggests a moderately long period of gestation; the largest females, which at this time were bearing young, presumably had contained embryos for several months. A similar situation holds also in the case of *Micrometrus minimus.*

4. The largest females, which produce young early in the season, were found to be in a spent condition, not containing a new lot of embryos, during the months of July and August. Although the data are less complete, this condition appears to hold also in the case of *Micrometrus.*

5. The fact that the smaller yearling females bear fewer young

than do the larger ones (as also in *Micrometrus minimus* and other embiotocids) suggests that fertilization is delayed for a considerable period subsequent to copulation. Now it is a well-known fact, in oviparous as well as in viviparous fishes, that the larger females of a given species are more prolific than smaller ones, and that is the situation in this family. In the present instance, however, it is presumed that the copulation preceding the development of the first brood of young (those carried by the yearling females under discussion) takes place soon after birth, when there is little variation in size or age (see preceding section). If fertilization were then immediately effected, some rather anomalous method of fertilization, or of egg production or resorption, would have to be postulated to explain why those females which would be smaller at the end of pregnancy bear fewer young than those females, which for some reason, early birth or otherwise, are destined to be larger when their young are ready for birth. But if it be assumed that fertilization is delayed for some time, until a considerable variation in size shall have arisen, the bearing of the fewer young by the smaller yearling fishes becomes no longer such a special problem.

6. Finally, the young males are sexually mature immediately after birth (see preceding section), at a time when they are associated only with the newly-born females, which apparently do not bear young until the next breeding season, one year later. A similar situation presumably holds in the cases of *Micrometrus minimus* and *Cymatogaster aggregatus.*

Embryonic Development and Natal Metamorphosis.

The developing embryos of the Embiotocidæ, in compensation for the reduced amount of yolk in the relatively minute egg, derive their nourishment almost entirely from the nutritive ovarian fluid in which they are bathed. This fluid, as Eigenmann (1894, etc.) determined, is circulated by the action of cilia through the embryos. The portion of the alimentary canal in which absorption chiefly takes place is doubtless the hypertrophied hind-gut, which in the embryos of *Amphigonopterus* and *Micrometrus,* as of other genera of the family, is a wide but thin-walled tube nearly filled with long, hollow, vascular villi. The respiration of

these embryos is seemingly largely effected over the surface of the body and fins, especially in the highly elevated vertical fins, in the distal dermal flaps of which the large interradial vessels form an extensive capillary net-work (cf. Ryder, 1885, 1893). The embryos, thus supplied with food and oxygen, pass through their development in the ovary, lying tightly packed against the ovarian walls and ovarian sheets, some directed forward, others backward, in such a fashion, as Agassiz long ago pointed out, as greatly to conserve space.

About the time of birth, the young of *Amphigonopterus* (and of other embiotocids) undergo a notable change, which may be termed the natal metamorphosis. The body becomes thicker, the flesh firmer; the vertical fins become shorter and less flexible, the interradial vessels smaller, the dermal flaps obsolete, and the hind gut more nearly normal in structure. The scales have already developed so far that they are widely imbricate, and the chromatophores have been formed in large numbers, but the body even in the largest embryos is very much paler in color than in the newly born young, particularly the males, which are even darker than the adults. In other species, as *Embiotoca lateralis*, and *Hypsurus caryi*, the latter as described by Agassiz, a sharply defined color pattern is developed before birth. The viviparous perches thus lose nearly all traces of embryonic peculiarities immediately before and after birth.

The young of *Amphigonopterus aurora* at birth vary in length approximately from 30 to 35 mm. (the caudal fin excluded), being about one third or one fourth as long as their mothers, as in other species of the family. Among several hundred examined early in June, the smallest free-swimming young was 29.0 mm. long, the longest unborn embryo, 35.5 mm. In a given series of embryos from one female, the variation in length is seldom more than one or two millimeters; thus the two sexes in *Amphigonopterus* are seen to be of at least approximately the same size at the time of birth; the differential rate of growth is wholly, or almost wholly, postnatal.

A female of *Embiotoca lateralis*, 257 mm. long to caudal, caught near Piedras Blancas, California, on June 2, contained 26 young 46 to 49 mm. long, not quite ready for birth. A slightly

larger female, 265 mm. long, collected in the same pool, also contained 26 young, but these were larger, 50 to 54 mm. long, and similar to recently born young obtained near Piedras Blancas, Pt. Sal and Pt. Arguello. Another female of this species, 200 mm. long and 125 mm. deep (exclusive of fins) contained only ten young, 55 to 58 mm. long, some having apparently been already born. The newly born young obtained, all during June, varied in standard length from 43 to 58 mm. A variation in size at birth of at least 16 mm. is thus suggested. Possibly, however, a slight decrease in actual length accompanies the metamorphosis of this species (as in *Albula vulpes* and the eels).

In the case of *Micrometrus minimus,* the extreme lengths of the embryos of a single female were found to differ normally from 0.0 to 3.0 mm. In three cases, however, the variation was much greater: in one lot of six embryos, the individual lengths were 5.5, 9.5, 10.8, 11.5, 14.3, and 14.7 mm.; in a second lot, five were 6.6 to 7.6 mm. long, a sixth, 2.7 mm.; in the third case, all but one of the fœtuses were 12.0 to 13.7 mm. long, the abnormal one being 9.0 mm. long, and provided with a strongly sigmoid vertebral column and a single eye, represented only by a mass of black pigment. Occasionally, a male embryo was found to be slightly larger or smaller than any of its fellows. If the 16 embryos in one female, 7 were males 16.3 to 18.7 mm. long, while 9 were females 17.0 to 18.0 mm. long; the average as well as the mean length for each sex was 17.5 mm. In another lot of 23 fœtuses from one female, 10 were males 20.0 to 22.3 mm. long (average length, 21.8 mm.), while 13 were females 20.4 to 23.0 mm. long (average length, 21.7 mm.).

Soon after birth the young of *Amphigonopterus aurora* leave the lower pools in which they were born, only a few remaining, probably for a very short time, in company with the breeding adults. They make their way thence into the pools accessible only at high tide, in such abundance that these pools, which are usually of small size and shallow, not infrequently harbor astonishingly large numbers of these young fishes. Such pools provide a large degree of seclusion from predatory enemies, as well as the warmest available water, in which the rapid growth of the first months may take place. This concentration and segregation

of the young may also be correlated with selective mating, especially in view of the natal maturity of the males.

Period of Breeding of Females of Different Size and Age.

The following table gives the average length of the young found in each of fifty one- and three-year-old[1] females of *Amphigonopterus*, all of which were obtained near Piedras Blancas, California, during the first week of June, 1916. Both adults and embryos were measured when freshly caught, prior to their preservation. The smallest young are not nearly developed to the stage at which they are born: it is improbable that the smaller females give little to young notably smaller than those of the larger females.

Table I.

Size of Young of Amphigonopterus aurora Carried by Females of Different Length and Age.

Average Length of Young (in mm. to Base of Caudal)	Lengths of Females Carrying Young of Foregoing Length.	Age of Females (End of Given Year since Birth).
12	77	I. (1)
13	96	I. (1)
14	85	I. (1)
15	84	I. (1)
16	76, 77, 82, 85	I. (4)
17	77, 86, 90, 95	I. (4)
18	78, 81, 84, 85, 88, 94	I. (6)
19	81, 87, 92	I. (3)
20	88, 88	I. (2)
21	92, 94, 95, 98, 98, 99	I. (6)
22	85, 87, 91	I. (3)
23	—	—
24	102; 122	I. (1); III. (1)
25	95, 103	I. (2)
26	103	I. (1)
27	102	I. (1)
28	95, 96; 118	I. (2); III. (1)
29	112	III. (1)
30	—	—
31	126	III. (1)
32	121, 123, 128	III. (3)
33	122, 123, 128	III. (3)
34	129	III. (1)

[1] The method of age-determination by scale examination will be discussed later.

The foregoing table indicates clearly—and the evidence has been confirmed by the writer by a study of material obtained at other localities—that *the smaller and younger females of Amphigonopterus give birth to their young later in the season than do the larger and older females.* This is true likewise of *Micrometrus minimus* (Table II.), and as Eigenmann (1894) has demonstrated, of *Cymatogaster* and other genera of the family (but Eigenmann made no definite age-determinations). This delayed breeding of the smaller, younger females of *Amphigonopterus* and other Embiotocids may be an advantageous adaptation, allowing the growth of the yearling females to be continued, as the structure of the scales indicates it does, during the breeding of the older females. Most of the females being one-year fishes in *Amphigonopterus* at least, this added growth would seem to admit of a material increase in the number of young produced.

Number of Young Born by Females of Different Size and Age.

The following table III., based upon data obtained from 48 breeding females of *Amphigonopterus aurora* (all obtained near Piedras Blancas during the first week of June, 1916), conclusively shows that *the smaller females bear fewer young than do the older and larger ones,*—

the one-year-old females with 5–9 young being 76–94 mm. long (average length, 83 mm.);

the one-year-old females with 10–15 young being 85–103 mm. long (average length, 96 mm.);

the 3- or 4-year-old females with 16–30 young being 121–129 mm. long (average length, 125 mm.).

Exceptional cases, excluded from this summary, are those of a three-year female with but 9 small young, and a one-year female with 19 young. Dr. Eigenmann (1894) has similarly found that the smaller females of several other species of the Embiotocidæ bear fewer young than do the larger ones, and the data presented in Table II. shows that this holds true in the case of *Micrometrus minimus.*

Table II.

Number and Size of Embryos of Micrometrus minimus Carried by Females of Given Age and Size (in Mm. to Caudal Fin).

Locality (Approximate).	Date.	Mother.		Embryos.	
		Age.	Size.[1]	Number.	Size.[1]
Monterey........	Mar. 26–Apr. 2	I.	59	7	3.7–4.3
"	"	I.	61	7	5.0–5.5
"	"	I.	65	7	5.0–6.0
"	"	I.	67	10	6.0–6.6
"	"	I.	71	9	4.6–5.4
"	"	I.	73	10	7.0
"	"	I.	74	10	7.6–8.3
"	"	II.	86	13	8.6–10.6
"	"	II.	92	17	9.3–10.2
"	"	II.	92	17	11.6–13.0
"	"	II.	92	19	11.6–12.7
"	"	III.?[2]	106	22	16.6–17.6
"	"	"	107	23	16.4–17.3
"	"	"	110	24	18.0–21.0
"	"	"	113	25	18.6–21.6
"	"	"	116	19	21.6–23.5
Avila............	May 25	III.?[2]	110	21	21.7–23.6
"	"	VI.?[2]	198	....	....
Piedras Blancas...	June 2	I.	58	3	5.3–5.5
" " ...	"	I.	60	2	4.6
" " ...	"	I.	60	4	6.7
" " ...	"	I.	61	6	10.0–10.4
" " ...	"	I.	66	8	7.4–8.9
" " ...	"	I.	67	7	10.0–11.8
" " ...	"	I.	70	6	5.5–14.7
" " ...	"	I.	70	8	12.7–13.4
" " ...	"	I.	71	9	12.3–13.0
" " ...	"	I.	73	8	12.2–12.5
" " ...	"	I.	74	8	15.0
" " ...	"	I.	76	12	9.0–13.7
" " ...	"	I.	79	10	16.0–18.0
" " ...	"	I.	79	13	15.7–17.7
" " ...	"	II.	85	15	15.0–17.0
" " ...	"	III.	97	16	16.3–18.7
Pt. Sal...........	June 17	I.	69	6	11.0–11.6
"	"	I.	72	6	2.7–7.6
"	"	I.	74	7	13.2–13.7
"	"	III.?[2]	96	17	17.0–18.3
"	"	V.?[2]	114	23	20.0–23.0
"	"	VI.?[2]	129	22	....
Pt. Purisima.....	June 18	I.	64	2	10.0
"	"	I.	67	6	8.3–9.3
"	"	I.	76	6	13.4–15.0

1 Preserved material measured.

2 Age uncertain, owing to the development of apparently accessory annuli.

TABLE III.

SIZE OF YOUNG CARRIED BY FEMALES OF DIFFERENT SIZE AND AGE.

Number of Young.	Lengths of Females Carrying Young.	Age of Females (End of Given Year since Birth).
5	87	I. (1)
6	76, 82	I. (2)
7	77, 77, 78, 79, 81, 84, 85, 87, 88	I. (9)
8	77, 81, 90	I. (3)
9	84, 85, 86, 88, 94; 122	I. (5); III. (1)
10	92, 96, 103	I. (3)
11	85, 88, 91, 95, 95	I. (5)
12	92	I. (1)
13	98, 98, 102	I. (3)
14	94, 95, 102	I. (3)
15	99, 103	I. (2)
16	129	IV. (1)
17	—	——
18	122	IV. (1)
19	96; 123	I. (1); III. (1)
20	122, 128	III. (2)
21	—	——
22	121, 128	III. (2)
23	123	IV. (1)
24 to 29	—	——
30	126	III. (1)

SEASONAL MARKS (OR ANNULI) ON THE SCALES.

During recent years there have been conducted numerous studies, of biological interest and economic significance, based upon age-determinations and the computed rate of growth of fishes. In these studies there has been developed and rather thoroughly tested a method of age-determination involving an interpretation of the seasonal rings indicated in scales, otoliths and certain bones; the scales have been most widely used. It has been demonstrated, most definitely in the salmonoid fishes, that the circuli covering the surface of the scales (cf. Fig. 4) become weaker in structure, more interrupted and more closely approximated during each winter, apparently as a result of the lessened physiological activity and retarded growth of the fish at that season. In certain fishes which have been investigated, these winter marks or *annuli* are indicated not so much by an approximation of the circuli as by a change in their direction and an interruption in

their course, along a line parallel with the scale margin (cf. particularly Taylor, 1914).[1] The reason for the formation of this type of annulus is the fact that the circuli toward the end of each year's growth gradually become more strongly curved, whereas those marking the new growth are straighter. This is the type of annulus formed on the scales of the Embiotocidæ (see Fig. 4),

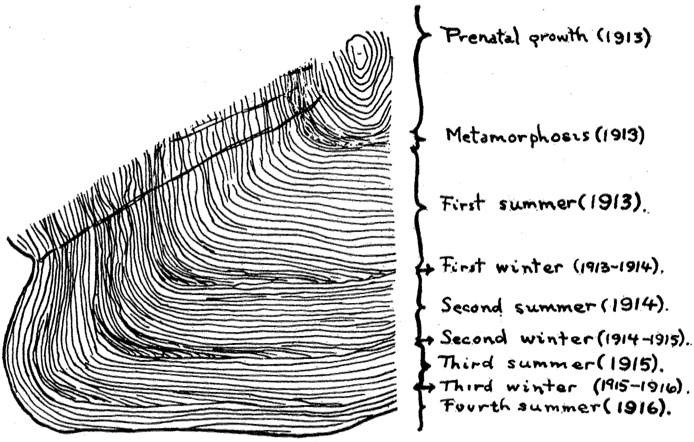

FIG. 4. Lateral field of a scale from a three-year-old female of *Amphigonopterus aurora,* showing the annuli.

although an approximation of the circuli is also frequently evident, especially on the basal and lateral fields.

That the annuli on the scales of *Amphigonopterus aurora* are formed during the winter is evident from a consideration of the following facts. A series of young from New Monterey collected on October 26, and another lot from near Pillar Pt., California, obtained on November 25, show no trace of an annulus at the margin of their scales, and had not yet attained the computed length at which this mark had been formed in larger specimens. Excluding recently born young, the smallest examples of either sex among those taken near Piedras Blancas during the first week of June, and also the young specimens secured near Pillar Pt. on April 1, have a single annulus on their scales, some dis-

[1] The statement by Taylor that no approximation of the circuli occurs in the annuli is partially erroneous (particularly as it applies to salmonoid fishes), as is also his conclusion that the annuli of the fishes which he studied were formed during the summer (even Taylor's own data indicates the contrary).

tance within the margin. Thus it appears that considerable growth had taken place since the annulus was formed. The actual amount of this growth (determined by a method discussed later), in 50 of the specimens from near Piedras Blancas, was estimated to have varied from 10 to 28 mm.; in more than half (28) of these the growth had been 14 to 18 mm., while the average growth computed to have occurred between the formation of the first two annuli of older fishes from the same locality, was about 24 mm. No annulus was found on the margin of the scales of gravid nor recently spent females, indicating that it is not a breeding mark.

In certain other species of the family, the annuli are doubled in a confusing fashion, suggesting the possibility that two annual checks in growth are registered on the scales, one during the winter and the other during the breeding season. For instance, the scales of a 200 mm. female of *Embiotoca lateralis,* taken on June 17, when bearing young, show five typical winter annuli, and in addition to these, and located between them, less distinct but similarly formed rings, the outermost at the extreme margin of the scales. Similarly in *Micrometrus minimus* the annuli are often closely approximated or doubled (beyond the second winter annulus); in these cases also the outermost annulus is located at the margin of the scales of females carrying young. Such a condition is seldom apparent in *Amphigonopterus,* but may have introduced an occasional error in the interpretation of the scales of the fishes three or four years old.

The annuli or seasonal rings on the scales of *Micrometrus minimus* closely resemble those of *Amphigonopterus aurora* (except in the more frequent appearance of doubled annuli, as just noted). The outermost annulus is located at some distance within the margin of the scales of yearling specimens taken in late spring and early summer in central California. In several specimens of both sexes, young of the preceding summer, taken at Pt. Loma on December 31, the single winter annulus is on or immediately within, in one male considerably within, the margin of the scale. These facts indicate that the annuli of *Micrometrus* are winter marks, that the first is formed in December in southern

California, and that there is some variation in the time of their formation.

Metamorphic Annulus.

The scales of even the largest embryos of *Amphigonopterus aurora* and of *Micrometrus minimus* are marked from focus to border by evenly spaced, concentric striæ; those of all but the most recently born young, on the other hand, are marked near the margin by a zone in which the circuli are finer and more closely approximated than on either side, and frequently angulated, their course on the scale within this zone being slightly different from that without. This mark, which is formed during the summer, resembles the winter checks or annuli formed farther out on the scales of older fishes, and perhaps quite as closely simulates the annulus on the scales of the Pacific salmon. As a distinctive name, the term *metamorphic annulus* is proposed for this mark. It is likewise indicated on the scales of *Cymatogaster aggregatus* and of other species of the family; the time of its formation (as indicated above soon after birth during the summer) has been confirmed in the case of *Embiotoca lateralis.*

The cause leading to the formation of the natal annulus is apparently a temporary retarding of growth immediately after birth, just as the other annuli are supposed to be formed as a consequence of the decreased nutrition and growth of the fish during the cold season. In this connection there should be recalled the sudden alteration of the method of feeding and respiration forced upon the young of these fishes at birth. They are then cast out into a very different medium, from which oxygen must be absorbed mostly through the gills, rather than through the skin and the tips of the fins. Instead of merely passing through themselves the nutritive fluid with which they were surrounded, they must now feed in the normal fashion of fishes. It is obviously these changes in the manner of living, which stamp a lasting mark on the scale. The metamorphic annulus significantly is usually more sharply evident in the males than in the females of those embiotocids known to be characterized by the natal maturity of the males.

Comparative Size of the Sexes at Different Ages.

Scales were retained from numerous specimens of *Amphigonopterus aurora* of measured length, all obtained near Piedras Blancas, California, on June 2 and 4, 1916. Excepting a few selected to represent extreme sizes, these were chosen at random from the large number collected. The annuli, discussed above, are well developed on these scales, their number indicating the approximate age of the fish (the time of intramaternal development, about one half year, being arbitrarily excluded). Thus the presence of a single annulus, in addition of course to the natal annulus, indicates that the fish was born in the preceding summer, and that it is just completing or has just completed, the first year

Table IV.

Length to Caudal Base of Females of Amphigonopterus aurora of Different Ages.

Age, One Year.		Age, Three Years.		Age, Four Years		Age, Five Years.		Age, Six Years.	
76 mm.	(1)	116 mm.	(1)	122 mm.	(1)	141 mm.	(1)	138 mm.	(1)
77	(3)	117	...	123	(1)				
78	...	118	(2)	129	(2)				
79	(1)	119	(1)	136	(1)				
80	...	120	(1)						
81	(3)	121	(1)						
82	(1)	122	(2)						
83	...	123	(1)						
84	(3)	124	...						
85	(4)	125	(3)						
86	(1)	126	(1)						
87	(2)	127	...						
88	(3)	128	(2)						
89	(1)								
90	(2)								
91	(1)								
92	(3)								
93	(1)								
94	(2)								
95	(4)								
96	(2)								
97	(1)								
98	(1)								
99	(2)								
100	(2)								
101	...								
102	(2)								
103	(2)								
104	...								
105	(1)								
106	...								
107	...								
108	(1)								

of its free-swimming life. As these fishes were obtained in the summer of 1916, those with three annuli were born in the summer of 1913, etc.

The collecting done near Piedras Blancas and at other localities indicated that the males average decidedly smaller than the females. It is of interest to have the field observations definitely confirmed by age-determinations.

TABLE V.

LENGTH OF MALES OF DIFFERENT AGES.

One Year.		Two Years.	Four Years.
59 mm.	(1)	82 mm. (1)	89 mm. (1)
60	(1)		
61	(1)		
62	(1)		
63	(1)		
64	(3)		
65	(4)		
66	——		
67	——		
68	(4)		
69	(2)		
70	(2)		
71	(1)		
72	(3)		
73	(1)		

The wide difference in the size of the two sexes of *Micrometrus minimus* as well as of *Amphigonopterus aurora* (Table VI.) appears to be of particular significance in the case of a small viviparous fish. The female of *Amphigonopterus* carries from 5 to 30 young which attain before birth more than one fourth the length of their mother, whereas the testes of the male are relatively small for a fish,—a fact determined by the conservation of spermatozoa, correlated with copulation (similar size relations prevail in certain other and probably in all embiotocids, and in many of the viviparous pœciliids). The differential rate of growth producing the relatively smaller size of the adult males is entirely or almost entirely postnatal, as previously indicated; in this connection it should again be recalled that at birth, only the males are mature.

Table VI.

The Comparative Size of the Sexes in Amphigonopterus aurora and Micrometrus minimus.

Species.	Approximate Locality (California).	Date of Collection.	Age (Winters).	Length in Mm. to Caudal.	Sex.	Number of Specimens.
A. aurora....	Piedras Blancas	June 2–4	I.	59–73	♂	25
" "	" "	"	I.	76–108	♀	50
" "	" "	"	II.	82	♂	1
" "	" "	"	III.	116–128	♀	15
" "	" "	"	IV.	89	♂	1
" "	" "	"	IV.	122–136	♀	5
A. aurora....	Pacific Grove	....	II.	134–139	♀	2
A. aurora....	Pillar Pt.	Nov. 26	0	48–70	♂	18
" "	" "	"	0	41–56	♀	17
M. minimus .	Pt. Loma	Dec. 31	I.	51–52	♂	2
" " .	" "	"	I.	63–64	♀	2
M. minimus .	Piedras Blancas	June 2	I.	52–62	♂	15
" " .	" "	"	I.	58–79	♀	14
" " .	" "	"	II.	66	♂	1
" " .	" "	"	II.	85	♀	1
" " .	" "	"	III.	68–71	♂	3
" " .	" "	"	III.	97	♀	1
M. minimus .	Pt. Sal	June 17	I.	62	♂	1
" " .	" "	"	I.	69–74	♀	3

Rate of Growth.

The rate of growth of a fish which develops seasonal marks on the scales can be readily computed with considerable accuracy from the known length of the fish at the time of capture and the measurements of one of its scales. The number of scales remaining constant throughout life, the scale increases in length along its horizontal axis in direct ratio to the increase in the length of the fish. Thus for a fish of given total length, the length attained at each winter, and consequently the growth increment of each successive year, may be computed by the use of the following formula:

$$\frac{\textit{length of fish at the time of capture}}{\textit{length of fish at winter } x} = \frac{\textit{length of scale to margin}}{\textit{length of scale to annulus formed in winter } x}$$

Several possible sources of error in the use of this formula are apparent. The scales do not develop until considerable growth has occurred. As the length of the scale is usually measured, for the purposes of growth computations, only from the focus cephalad to the basal margin, an unequal growth of the different fields of the scales may introduce an error. There is some variation in the time of formation of the annuli. The scales often overlap less widely in young fishes than in adults, rendering the computation of size for the first winter too small. Again, the length of the fish is measured, for growth computations, from the tip of the snout to the base of the caudal fin. There is thus included the length of the head, which becomes relatively shorter with increased size in most fishes. As the formula assumes that the head and body increase in the same ratio, the computed length for the young fish at a given stage would be accurate only if the head were then of the same proportional length. The head being relatively longer, however, the computation is too small. It is doubtless these factors (probably all of them) which have rendered the computed length of the young of *Amphigonopterus* at the time of the formation of the natal annulus (just after birth) to be less than the observed length at that stage (20 to 32 mm., instead of 29.0 to 35.5 mm.).

Table VII.

Computed Rate of Growth of Females of Amphigonopterus aurora.[1]

Period of Growth.	Growth.	Specimens
To formation of natal annulus	20–32 mm.	70
Thence to end of first winter	29–68 mm.	69
Between first and second winters	14–35 mm.	20
Between second and third winters	12–27 mm.	20
Between third and fourth winters	13–18 mm.	5
Between fourth and fifth winters	13 mm.	1
Between fifth and sixth winters	4 mm.	1

[1] Based upon material collected near Piedras Blancas during the first week of June, 1916.

It is evident from these figures, as well as from supplementary data obtained from collections made on other occasions, that *the growth of the first half year (between birth and the first winter) is greater than that of any subsequent whole year.* This estimate

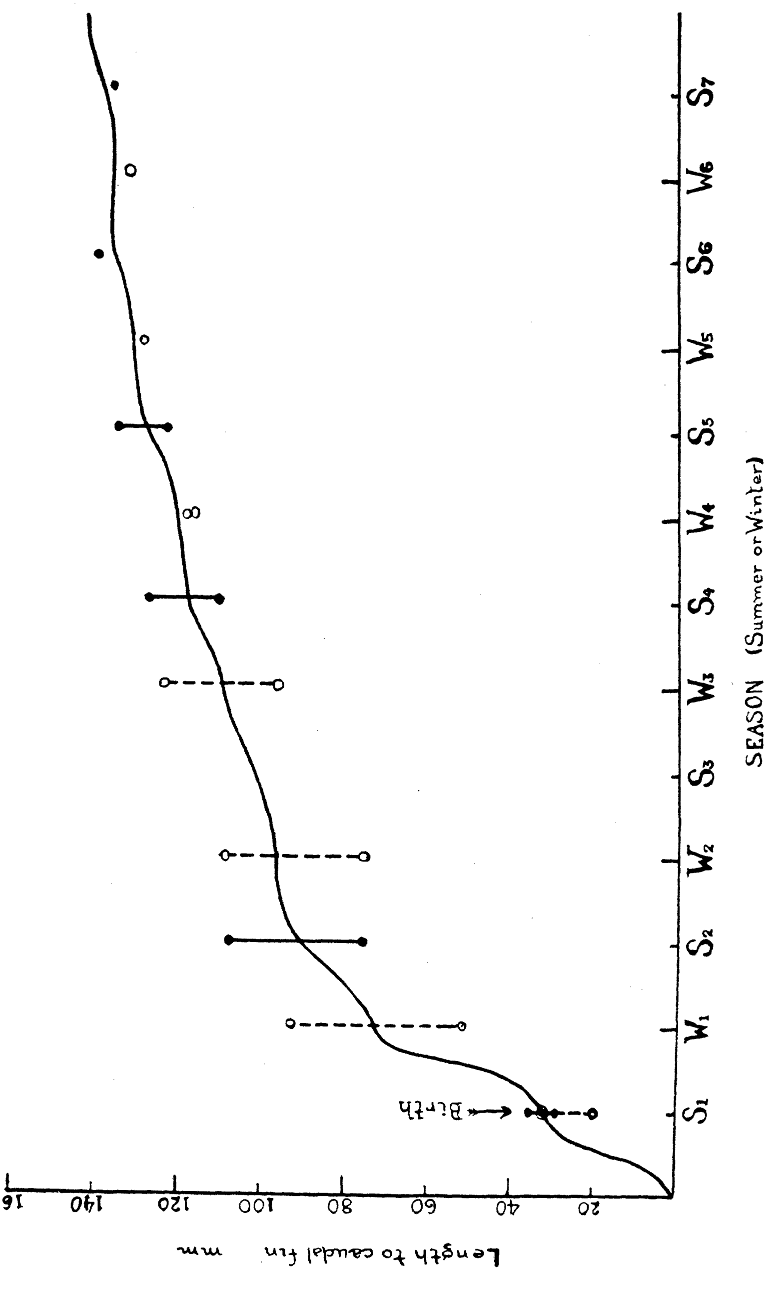

FIG. 5. Estimated average growth curve of females of *Amphigonopterus aurora* on the reefs of San Luis Obispo County, California. Lengths for summers obtained by measurement of specimens collected on June 2–4, 1916; lengths for winters obtained by computation from scale-measurements of the same fishes.

appears particularly significant, in view of the fact that the females become pregnant at or immediately after their first winter. As usual in fishes, their is no evidence that the growth ever wholly ceases during life, although it is markedly and increasingly retarded with age.

The growth of the single four-year-old male of *Amphigonopterus* obtained near Piedras Blancas was computed from the direct ratio of scale length to fish length. The length of the head and body to the end of the formation of each annulus was thus estimated to have been as indicated below.

Length at end of formation of natal annulus	26 mm.
" " " " " " first winter annulus	50 mm.
" " " " " " second winter annulus	63 mm.
" " " " " " third winter annulus	73 mm.
" " " " " " fourth winter annulus	84 mm.
" " " " fourth year (on June 4, 1916)	89 mm.

The growth of this male, although slower, was quite similar to that of the females, being greater between birth in the summer and the first winter, than during any subsequent whole year; the check in growth rate in this case follows the second, rather than as usual the first, period of breeding.

The writer has found but one published record of a direct observation on the rate of growth of a viviparous perch. It was made on aquarium fishes by the late Charles Frederick Holder, and published anonymously and without identification of species.[1] The obscure but pertinent passage is as follows. "The young, ten or twenty in number, born in the summer, are from an inch and a half long at birth, and attain half their adult size the first winter, and their full growth in about two and a half or three years." Dr. Eigenmann (1894) has remarked on the large size of the smaller breeding females of *Cymatogaster,* which he correctly assumed to be one year old. A similar rate of growth holds in the case of *Micrometrus minimus.*

In the course of his extensive investigations of the life-history of the sockeye salmon (*Oncorhynchus nerka*), Dr. C. H. Gilbert

[1] Another note by the same author makes it evident that the species observed was *Cymatogaster aggregatus* (see Bull. U. S. Bur. Fish., Vol. 28, 1908 (1910), p. 1139).

(1914, pp. 61–71) has induced an important generalization, *the law of growth compensation.* Those salmon which grow most in their first year (as a result of earliest hatching or of other causes), tend on the average to grow least in their succeeding years, while those which have attained a relatively small size at the end of the first year, grow with accelerated speed during the next years. The physiological mechanism of the salmon appears to regulate its growth in such a fashion that the length of the adult fishes of each race varies but little. It was hoped that it might be determined whether this law of growth applies to *Amphigonopterus,* but so few fishes more than one year of age were examined, that the data are incomplete. The evidence being suggestive, however, is presented in the following table (based upon the material from Piedras Blancas).

TABLE VIII.

COMPUTED LENGTHS OF TWENTY 3- TO 6-YEAR-OLD FEMALES OF AMPHIGONOPTERUS AT THE END OF FIRST THREE WINTERS.

	Length at End of First Winter.	Length at End of Second Winter.	Length at End of Third Winter.
	52	76	97
	58	91	108
	61	94	109
	62	93	107
	62	96	121
	63	98	110
	64	80	100
	67	101	115
	67	94	113
	68	82	109
	72	93	113
	74	101	120
	75	103	119
	77	101	120
	79	98	124
	80	108	120
	81	96	118
	83	103	120
	85	99	111
	93	109	124
Variation	52 to 93	76 to 109	97 to 124
Range	41	33	27
$\frac{\text{Range}}{\text{Mean}}$	.57	.40	.26

It appears probable that the variation in size of *Amphigonopterus* at the end of the third winter is less than at the end of the

first winter; that the principle of growth compensation is applicable to this embiotocid. Similar data gathered from one-year-old females strengthen this conclusion.

TABLE IX.

COMPUTED SPRING GROWTH OF SPECIMENS WHICH HAD ATTAINED EITHER A SMALL OR A LARGE SIZE AT THEIR FIRST WINTER.

Length at End of Formation of First Annulus.	Spring Growth (in Millimeters).																		
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Less than 75 mm..........	–	–	1	–	3	1	2	5	3	–	2	4	2	1	1	–	–	–	1
More than 75 mm.........	1	1	2	2	1	6	1	3	2	2	1	–	–	–	1	–	–	–	–

BIBLIOGRAPHY.

Note: Eigenmann (1894) has given an extensive bibliography and a discussion of the earlier contributions pertinent to the viviparity and embryology of the Embiotocidæ. Only the later references need therefore be listed here. Additional papers by the same authors may be located with the aid of Dean's *Bibliography of Fishes*.

Eigenmann, Carl H.

'94 On the Viviparous Fishes of the Pacific Coast of North America. Bull. U S. Fish Comm., Vol. 12, 1892, pp. 381–478; pls. 92–118.

'95 Development of Sexual Organs in *Cymatogaster*. Proc. Indiana Acad. Sci., 1894, p. 138.

'96 The history of the Sex-cells from the Time of Segregation to Sexual Differentiation in *Cymatogaster*. Trans. Amer. Micros. Soc., Vol. 17, pp. 172–173.

'96a Sex-differentiation in the Viviparous Teleost *Cymatogaster*. Arch. Entwick.-Mech. Organ., Vol. 4, 1896, pp. 125–179; 6 pls.

'96b The Bearing of the Origin and Differentiation of the Sex Cells of *Cymatogaster* on the Idea of the Continuity of the Germ Plasm. Amer. Nat., Vol. 30, pp. 265–271.

Eigenmann, Carl H., and Ulrey, Albert B.

'94 A Review of the Embiotocidæ. Bull. U. S. Fish Comm., Vol. 12, 1892, pp. 382–400.

Gilbert, C. H.

'14 Contributions to the Life-history of the Sockeye Salmon. (No. I.) Rept. Comm. Fish. Brit. Col., 1913, pp. 53–78, 9 plates.

Holder, Charles Frederick.

No date [Avalon] Aquarium Guide. Animals of the Submarine Gardens Santa Catalina (no pag.).

Hubbs, Carl L.

'17 The Breeding Habits of *Cymatogaster aggregatus*. Copeia, No. 47, pp. 72–74.

'18 A Review of the Viviparous Perches. Proc. Biol. Soc. Wash., Vol. 31, pp. 9–13.

Jordan, David Starr.

'05 Guide to the Study of Fishes, 2 vols. [viviparity in fishes: Vol. 1, pp. 124–130, Figs. 91–96.—Embiotocidæ: Vol. 2, pp. 372–379, Figs. 306–312].

Jordan, David Starr, and Evermann, Barton W.

'98 The Fishes of North and Middle America. Bull. U. S. Nat. Mus., No. 47, pt. 2 [Embiotocidæ, pp. 1493–1511].

'00 *Ibidem,* pt. 4, plates [Embiotocidæ: Figs. 577–586].

Taylor, Harden F.

'16 The Structure and Growth of the Scales of the Squeteague and the Pigfish as Indicative of Life-history. Bull. U. S. Bur. Fish., 34, 1914, pp. 287–330, Figs. (bibliography).